# The Role of Chemicals in Host-Searching Behaviour

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*Parasites follow chemical trails to find their hosts. In a tritrophic system, parasitoids use infochemicals in host-searching behaviour. Plants that the hosts feed upon constitute the third member of this parasitoid-host-plant complex. Turlings et al. (1991) isolated 11 volatiles attractive to the parasitoid wasp* Cotesia marginiventris. *They found none of these volatiles emanating from the host larvae; instead, nearly all infochemicals originated from plants. This release of infochemicals is the plant's defensive action against larval infestation.*

### Introduction

Parasites make their living by taking resources from their hosts without giving anything in return. Indeed, hosts often die from parasitic infestations. Potential hosts, therefore, tend to develop defenses against parasites, and parasites counter host defenses by finding alternative strategies. Host-searching strategy may be one of these cat-and-mouse games. Though host species tend to minimize them, chemical cues play an important role in the host-searching behaviour of parasites.

### Host-Searching Examples

The cues parasites use to track hosts are normally chemicals the host has little control over. Tsetse flies (Glossina palpalis), for example, respond to $CO_2$ while looking for blood sources (Bogner 1992). They have receptors sensitive to $CO_2$ concentrations greater than that of air (~0.03%). This is a good tracking cue for the tsetse since respiring hosts can hardly control their $CO_2$ exhalation.

The chemical tracks followed by parasites can also exist on substrates. Haberl and Haas (1992) discovered the signals used by the human body fluke (Schistosoma mansoni) to find its intermediate snail host (Biomphalaria glabrata). Besides $MgCl_2$, they found S. mansoni is attracted to a 300Kd glycoconjugate found in snail conditioned water.

Herbivorous insects, too, use chemical cues. The true fruit fly Rhagoletis pomonella both eats, and lays eggs in, specific species of apple. R. pomonella finds its host by following wind-borne fruit volatiles (Aluja and Prokopy, 1992). They find apple by flying upwind and following the odor plumes of ripe fruits.

Of special interest to agriculture is the parasitoid Cotesia marginiventris. This parasitoid wasp attacks, and causes high mortality in, larvae of agricultural pests. During the attack, the female wasp lays her eggs inside host larvae; the wasp larvae then feed and grow until they emerge from their host as adults. C. marginiventris use both volatile and contact chemical cues to find their hosts. These wasps are part of a chain involving the parasitoid, its host, and the host's food plant.

### Terminology

Early studies of chemical interactions between organisms focused on bitrophic systems only. Modern research involving tritrophic systems have added confusion to the terminology developed earlier. Therefore, Dicke (1988) proposed updated terminology for infochemicals. Table 1 shows the definitions for terms used here. Note that infochemicals may fit more than one definition. A pheromone, for instance, may also act as a kairomone.

> ***Infochemical***: *A chemical conveying information in an interaction between two individuals, evoking a behavioural or physiological response in the receiver.*
>
> > ***Pheromone***: *An infochemical mediating an interaction between organisms of the same species whereby the benefit is to the origin-related organism [(+, -) pheromone], to the receiver [(--, +) pheromone], or to both [(+, +) pheromone].*
> >
> > ***Allelochemical***: *An infochemical mediating an interaction between two individuals belonging to different species.*
> >
> > > ***Allomone***: *An allelochemical pertinent to the biology of an organism (organism 1) and that, when contacting an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response adaptively favorable to organism 1, but not organism 2.*
> > >
> > > ***Kairomone***: *An allelochemical pertinent to the biology of an organism (organism 1) and that, when contacting an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response adaptively favorable to organism 2, but not organism 1.*
> > >
> > > ***Synomone***: *An allelochemical pertinent to the biology of an organism (organism 1) and that, when contacting an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response adaptively favorable to both organism 1 and 2.*

## The Tritrophic System

Systems described here are generally tritrophic--feeding systems involving three levels. This is in contrast to a bitrophic system involving only two levels--a producer and a consumer. A tritrophic system normally involves a plant as the primary producer, a host that feeds on the plant, and a parasite using the host. Figure 1 shows the general relationship among these three, along with a typical example.

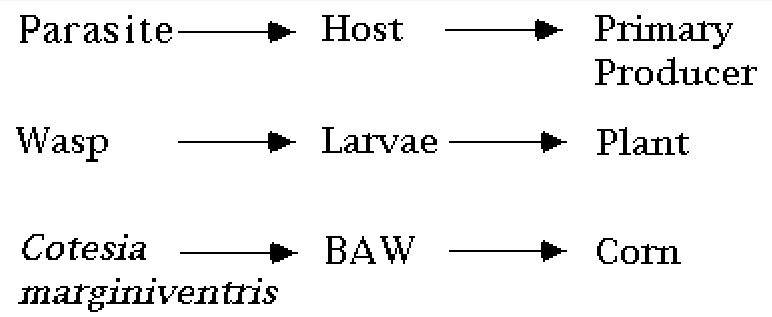


**Figure 1. A tritrophic system. Arrows point toward the 'used' organism. The top line shows a general relationship, the middle line demonstrates an insect-plant system, and the bottom line shows the particular system studied by Turlings et al. (1991). BAW is the beet armyworm.**

## Isolated Volatiles

Until recently, no one had identified the individual chemicals involved in host-searching behaviour. Early experiments used substances thought to contain parasitoid-attractive chemicals. They used simple Y-tubes, containing plant, or host parts, to measure the response of parasitoids. If the parasitoid visited one substance more than another, then the parasitoid was thought to be following an infochemical. These test substances could be damaged leaves, or scales from a host's ovipositor; they also contained, of course, many unidentified chemicals. In 1991, Turlings et al. isolated and identified 11 kairomones attractive to *C. marginiventris*.

To isolate these volatiles, Turlings et al. collected chemicals from several potential sources, then tested their attractiveness to *C. marginiventris*. The most attractive volatiles were then isolated and identified. Figure 2 shows the chemical structure of these 11 chemicals.

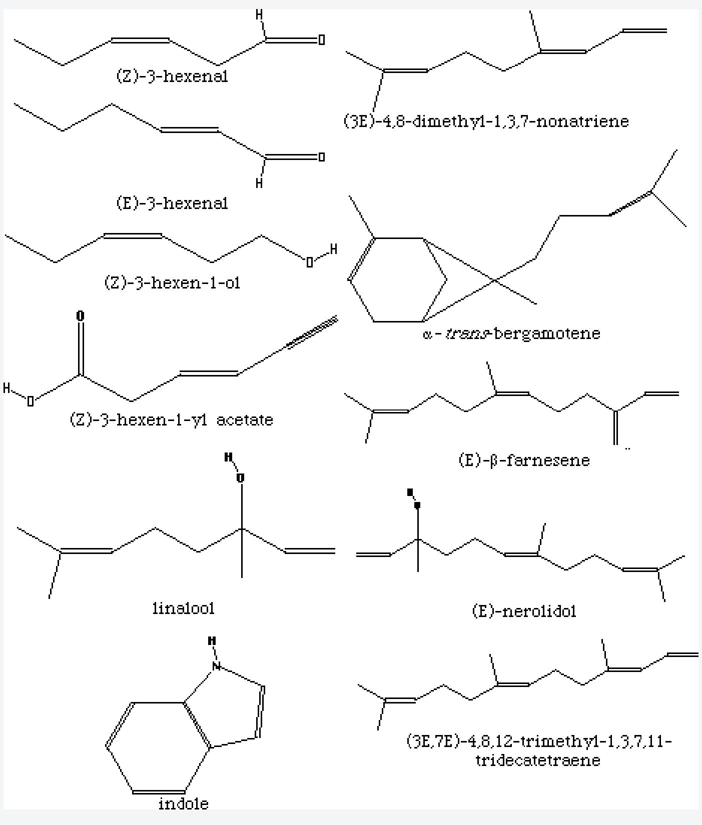


**Figure 2. Infochemical structure. The 11 major compounds identified by Turlings et al. (1991). They collected these volatiles directly from an airstream passed over the odor source. These odor sources consisted of damaged corn seedling leaves, beet armyworm (BAW) feces, and starved water-washed BAW caterpillars. Chemical Sources Understanding multitrophic systems entails not only identification of infochemical structure, but also identification of their sources. In a given parasitoid-host-plant complex, the kairomone trails followed by the parasitoid to its host may originate from any of three sources. The kairomones could come from the host, host products such as scales lost during ovipositing, or the plant serving the host. Some parasitoids, moreover, deposit infochemicals to distinguish between parasitized and unparasitized hosts, thus preventing superparasitism.**

### Host Sources

A parasite able to find its host, might be following cues emanating either directly from the host itself or from discarded host products. These products include feces, scales, oral secretions from caterpillars, or pheromones. To test these sources, Turlings et al. performed flight-tunnel bioassays using C. marginiventris and beet armyworms (BAW). They tested BAW caterpillar feces collected from BAW-infested corn seedling leaves, and water-washed BAW caterpillars. Female C. marginiventris responded only to damaged leaves. Furthermore, using chromatographic techniques, they discovered that neither BAW feces nor caterpillars showed any trace of the 11 volatiles (see Fig. 2).

### Plant Sources

Damaged leaves did, however, release 9 of the 11 volatiles in Figure 2. Since Turlings et al. found no volatiles in the hosts, then plants must be the main source of these chemicals. Indeed some of these chemicals are not found in animals at all; they occur only in plants. Research in other tritrophic systems has also found several plant-derived infochemicals. Chemicals found in certain night-scented flowers attract moth pollinators (Dicke 1990). Both lima bean leaves and cucumber leaves produce volatiles during spider mite infestations (Dicke 1988). Turlings et al. found no volatiles emanating from undamaged plants. This is further evidence that plants are the main source of kairomones in tritrophic systems. They showed this by using both flight-tunnel bioassays and chromatography. Moreover, Lewis and Martin (1990) showed that artificially damaged plants generate host-searching responses in several other parasite species. Though the kairomones used by parasitoids during host-searching behaviour originate in plants, the host my have incorporated these chemicals into some of their own body parts. Only host larvae (Heliothis zea) raised on cowpea plants, for example, will cause a positive response in C. marginiventris. Larvae fed on other foods do not attract the wasps.

### Parasite Behavioural Responses

Kairomones can cause complex behavioural responses in parasitoids. In finding their host, they must follow both volatiles and substrate bound chemicals. When sensing one of these chemicals, the parasite may initiate a search pattern for hosts, possibly switching from one kairomone to another along the way. Upon kairomone contact in moth scales, for example, some parasitoids significantly increase their local searching activities. Parasitoids have a remarkable sensitivity to kairomones. In their flight-tunnel bioassays, Turlings et al. used both the natural-source odors and their isolated synthetic volatiles (Fig. 2). Though C. marginiventris followed both types of chemicals, the wasps preferred natural odors. Moreover, these wasps can distinguish between the different kinds of damage to leaves caused by two different species of noctuid larvae (Lewis and Martin, 1990). Parasitoids able to detect only a narrow set of kairomones, however, might be susceptible to defensive changes made in the chemicals by the host or the plant. Parasitoids would be left without a host if they could not keep up with these changes. Parasitoids, therefore, show great variation in their behavioural responses to kairomones.

### Parasitoid Behavioural

Variations To counter environmental changes, including host variations, parasitoids show significant variation in their response to kairomones. These variations occur in three categories: genetic diversity, phenotypic plasticity, and physiological state (Lewis and Martin, 1990).

### Genetic Diversity

Parasitoids have considerable genetic diversity in their response to kairomones and this diversity is heritable. These parasitoids, therefore, are better able to adapt to environmental variations.

### Phenotypic Plasticity

Parasitoids can learn to recognize new kairomones, and their response to these kairomones is modified by this learning. They can develop preferences for kairomones after exposure to them. Turlings et al. found that although C. marginiventris originally preferred natural odors, they eventually showed equal responses to the synthetic chemicals after repeated exposure. Some species of parasitoids are able to learn the chemical cues of a potential host by antennating the host's feces. They then recognize these new infochemicals as indicating the presence of a host.

### Physiological State

Needs such as general health, mating, and food can also influence a parasitoid's host-searching behaviour. Any of these requirements may become more important than egg deposition. Moreover, the female parasitoid may not even have any eggs ready to deposit in a host.

### Plant Communication

Plants damaged by hosts are the main source of parasitoid-attractive kairomones--not the hosts themselves (Turlings et al.). It is, of course, in the host's best interest to eliminate any chemical attractants. But why would plants release these substances? Might not hosts also follow these chemical trails to the plant? Undamaged plants do not emit any of the 11 volatiles in Figure 2. Turlings et al. found the volatiles only when leaves were damaged, either by hosts or artificially. This suggests a reason for the plant-derived kairomones. Host species can cause severe damage to the plants they infest. It is, therefore, in the plant's best interest to rid itself of these pests. Plant release of kairomones is a defensive call to parasitoids! These volatiles are a direct defense against attackers. Furthermore, these chemicals can produce defensive responses in neighboring plants. Other plants "overhear" an infested plant's cry for help and begin producing these synomones themselves. This means the plants are talking to each other to better repel attacking larvae!

### Agricultural Applications

The knowledge of the role of kairomones in host-searching behaviour can be applied to agriculture. Kairomones might be spread about a crop to help attract parasitoids and control the damage due to host pests. Additionally, plants might be genetically engineered to produce, and export to their leaf surfaces, kairomones attractive to the pest's parasitoids. Technology is now emerging in this area (Lewis and Martin, 1990).

### Conclusion

Kairomones are important signals in the host-searching behaviour of parasitoids in a tritrophic system. Parasitoid host-searching behaviour is capable of changing in response to variations in these chemicals. However, this is not a measure-countermeasure scenario between the host and the parasitoid. The host's defense is to emit as little attractant as possible. These signals originate not from the host larvae, but from the plant upon which the host is feeding. When under attack, plants dramatically increase their release of volatiles, thus attracting parasitoids. Synomones in this sort of tritrophic system, therefore, are a defensive action against infestation. Furthermore, these chemicals can signal other plants to release synomones to effect a community defense.

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